Life history of the Imperial Moth *Eacles imperialis* (Drury) (Saturniidae: Ceratocampinae) in New England, U.S.A.: distribution, decline, and nutritional ecology of a relictual islandic population

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Abstract. The decline and current status of *Eacles imperialis* (Drury) (Saturniidae: Ceratocampinae) in New England are reviewed, and primary data surrounding the life history and nutritional ecology presented. Though common throughout much of its historical North American range, this species declined precipitously in New England during the 20th century. Suggested explanations for this region-wide decline include the deployment of pesticides and metal halide street lamps and the introduction of parasitoid flies. The existence of a remnant population of *E. imperialis*, thought to have been extirpated from New England as early as the 1950s, is reported from Martha's Vineyard Island, Dukes County, Massachusetts, U.S.A., representing the last relict of a phenotypically, phenologically, and possibly ecologically infrasubspecific entity. Based on comparisons with museum specimens, adults from this population appear to be indistinguishable from the few historical specimens known from nearby mainland Massachusetts, smaller than those from now extirpated populations in Connecticut, New York, and New Jersey, and slightly larger than members of, the northernmost *E. imperialis* populations (*E. i. pini* Michener) found in the Great Lakes region. The Martha's Vineyard population is univoltine, peaking in late July and exhibiting a more contracted flight season than other extant North American populations. Both parentage and food plant significantly affect larval growth and development, and although larvae on Martha's Vineyard feed extensively if not exclusively on pitch pine (*Pinus rigida*) in the wild, they grow significantly faster, attain greater pupal weights, and more efficiently convert ingested and digested tissues of post oak (*Quercus stellata*) to biomass in the laboratory. Performance as measured by relative growth rate and the efficiency of conversion of ingested and digested food to biomass (ECI and ECD) are correlated with foliar nitrogen and water content: post oak foliage during the larval growth season contains more nitrogen and water than corresponding amounts of pitch pine foliage growing in the same soils. It is suggested that there exists a non-nutritional explanation for the association of *E. imperialis* with pitch pine and for its pattern of decline and persistence. The taxonomic and possible biogeographic affinities of this population are discussed from within the context of a growing understanding of New England's diverse yet threatened lepidopteran fauna, and the potential for reintroducing *E. imperialis* to mainland New England is discussed.

Key words: *Eacles imperialis*, invertebrate conservation, Martha's Vineyard, pitch pine.

INTRODUCTION

The imperial moth *Eacles imperialis* (Drury) (Saturniidae: Ceratocampinae), is one of North America's largest and familiar saturniids. Throughout its extensive range, this species exhibits considerable regional variation in coloration and size—on the basis of which three North American subspecific epithets are currently attributed—as well as variation in phenology and host plant utilization (Ferguson, 1971; Covell, 1984; Tuskes *et al.*, 1996). Considered a common moth in the southern United States, *E. imperialis*, like many large bombycoid moths, underwent a precipitous decline in much of northeastern North America during the mid-20th century (Hessel, 1976; Ferguson,

1971; Schweitzer, 1988). Ferguson (1971: 25) writes "[the imperial moth]...like some of the other large saturniids, is said to have largely disappeared from heavily populated areas such as those in Connecticut and the vicinity of New York City, where it was formerly common." Various hypotheses for such declines, ranging from the expanded use of metal halide bulbs in street lamps (Hessel, 1976) to the widespread deployment of pesticides aimed at gypsy moths (Goldstein, 1991) and to the introduction of parasitoids, specifically the tachinid fly *Compsilura concinnata*, for the same purpose (Boettner *et al.*, 2000) have been invoked to explain these declines. Believed extirpated from New England, a relict population of *E. imperialis* was verified by the author in 1982 on Martha's Vineyard Island (Dukes Co.), off Cape Cod, Massachusetts, where it quickly became of interest to conservationists. In this paper, following a

review of the taxonomy and regional variation in this species complex, I present life history observations and larval growth and performance data on this population between 1986 and 1989, discuss this species' decline by summarizing historical records and information on pesticide deployment and parasitoid impacts, and discuss the nutritional and life history requirements of this species in light of putative reestablishment on mainland New England.

Distribution and variation in the *Eacles imperialis* complex in North America

Extending from Canada to Argentina, the imperial moth *E. imperialis* is both the widest-ranging and the northernmost occurring species in its genus and one of the most widely distributed saturniids that occurs in North America (Lemaire, 1988), representing a complex of ecologically and possibly phylogenetically distinct intra-nominal entities. Authors have differed in their treatment of subspecific epithets, variously recognizing the western *E. oslari* as a full species versus a subspecies of *imperialis* and the southern *E.i. nobilis* Neumoegen as a subspecies versus a synonym of nominate *imperialis* (reviewed in Tuskes *et al.*, 1996). Not including these, two recognized subspecies of *E. imperialis* occur in North America (Lemaire, 1988; Tuskes *et al.*, 1996): the nominate subspecies and *E. i. pini*, which is distributed in the Great Lakes region and the Adirondacks.

According to Ferguson (1971: 24), *E. imperialis* "occupies nearly all of the United States east of the Great Plains, with the exception of northern New England and northern portions of Michigan and Wisconsin." Ferguson (1971: 25) further reports records "from southern New Hampshire...through New York State, the Niagara Peninsula of Ontario, and southern Michigan, westward to the eastern edge of the Great Plains, and southward to the Gulf Coast and southern Florida (but not the Florida Keys). It has not been taken in Maine." The New England states are represented by specimens in collections at the American Museum of Natural History (AMNH), the Museum of Comparative Zoology, (MCZ), the Peabody Museum of Natural History (PMNH), which houses the bulk of the F. M. Jones collection from Martha's Vineyard, and the collection of the now defunct Boston Society of Natural History (BSNH), which currently resides at Boston University (Fig. 1). A single 1900 specimen from Kittery Point (southern Maine's York County) is housed at the MCZ, and Patch (1908; cited in Tuskes *et al.* [1996: 65]) reported it from Cumberland County, ME. Beyond these records, Farquhar's (1934) thesis enumerated various other
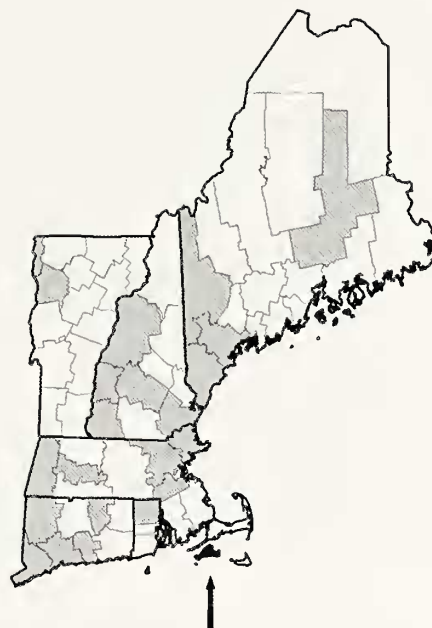

Figure 1. Historical distribution of *E. imperialis* in New England by county. Arrow indicates presence of lone extant population on Martha's Vineyard Island, Dukes Co., MA.

New England records, also included in Fig. 1.

The species' current occurrence in the northeastern portion of its range south of New England, including Long Island, N. Y. and southern New Jersey, is associated at least in part with habitats characterized by sandy soils such as pitch pine-scrub oak barrens, where its larval host plant, pitch pine (*Pinus rigida*), abounds. Such habitats have been heavily impacted, in large part due to the ease with which sandy soils are manipulated for building and construction purposes. Sandy, well-drained soils may be a requirement for *Eacles imperialis* in that, like all ceratocampine saturniids, *Eacles* larvae do not construct cocoons but burrow into and pupate within the soil, from which the pupae themselves emerge so that the adults may eclose above-ground. The conspicuous dearth of historical records from Cape Cod, where sandy soils predominate, may be attributable to a combination of small private collections' having been orphaned.

Eacles imperialis exhibits apparently clinal variation in wing maculation and shading as well as in size and phenology, with southern populations (formerly attributed to *E. i. nobilis*) often exhibiting more intense brown postmedial shading than northern populations. It has also been observed that adult individuals of northern populations attributed to *E. i. pini* in

northern Michigan , Ontario, Quebec, and New York, are markedly smaller than their southern and eastern counterparts (Ferguson, 1971; Tuskes *et al.*, 1996), and bear more intensive peppering with blackish spots; the larvae exhibit pronounced dorsolateral scoli relative to nominate *imperialis*. The maculation on specimens taken from Martha's Vineyard is consistent both with museum specimens from the island and with those taken from mainland New England prior to the species' decline there. Based on an examination of these and other specimens from the northeast, the mean forewing length for male *E. imperialis* from Martha's Vineyard was 49.64 mm (N = 60, se = .401), significantly smaller than that of 78 specimens examined from New York, Connecticut, and New Jersey (one-way ANOVA, p < .0001, DF = 1, F-ratio = 88.241; Fig. 2), and at the lower end of the range of 47.59 mm reported by Tuskes *et al.* (1996). This number is higher than the average male wing length of 47 mm reported for *E. i. pini* by Michener (1950) in the original description and out of the 42 mm - 48 mm range reported for male *pini* by Tuskes *et al.* (1996). Michener (1950) also reported an average wing length of 54 mm for male nominate *imperialis* from the vicinity of New York City; specimens I measured from this area averaged 54.92 mm (N = 36, se = .92), by way of comparison. Although female wing lengths for mainland New England specimens were not analyzed due to their scarcity in collections, Martha's Vineyard female specimens averaged 57 mm in wingspan, just below the range of 58-68 mm reported by Tuskes *et al.*, greater than the 51 mm average *pini* female wingspan reported by Michener and out of the 47 mm - 54 mm range reported for *pini* by Tuskes *et al.*

The familiar green/brown larval polymorphism of *E. imperialis* is apparent both among lab-reared caterpillars and those observed in the wild on Martha's Vineyard. Both maternity and food plant affect the expression of this polymorphism: among the larvae reared for this study and in situ (P. Goldstein, unpubl.), the lime green color form was less prevalent than the dark brown, with the majority of reared green larvae developing on pine versus oak. Ferguson (1971: 26) writes that "[a] brood from Massachusetts, described by Eliot and Soulé [1902], contained only one green larva." Harris (1890: 404), on the other hand, writes "[the caterpillars are] for the most part, of a green color, slightly tinged with red on the back; but many of them become more or less tanned or swarthy, and are sometimes found entirely brown." During the course of my rearing, I observed seven cases in which larvae switched from brown to green at one molt only to shift back at a subsequent molt; a common color morph of oak-fed larvae. The most common color morph
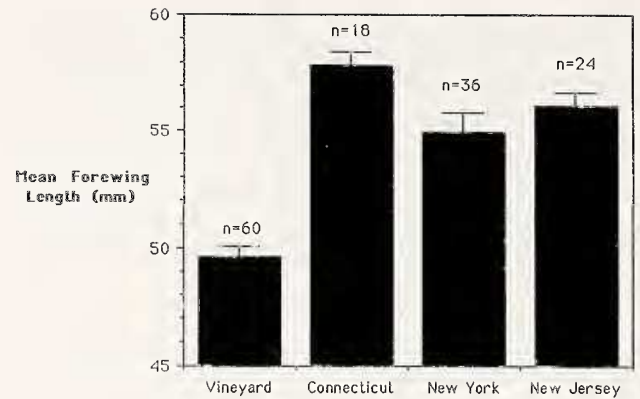

Figure 2. Mean forewing length (base to apex, in mm) of 138 male *Eacles imperialis* from Martha's Vineyard, Connecticut, New York, and New Jersey. The mean forewing length for male *E. imperialis* from Martha's Vineyard was 49.64mm (N=60, se=.401), significantly smaller than that of specimens examined from New York, Connecticut, and New Jersey (one-way ANOVA, p<.0001, DF=1, F-ratio=88.241). See text.
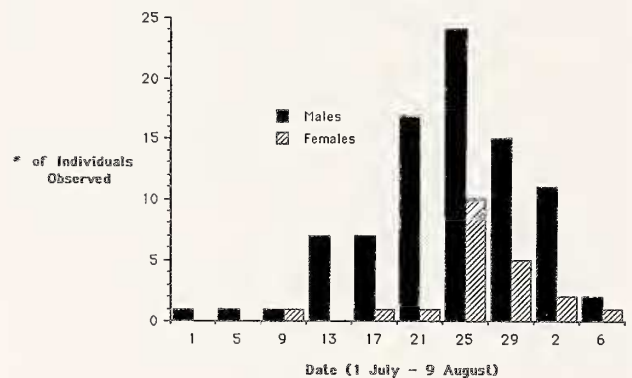

Figure 3. Flight season of *E. imperialis* on Martha's Vineyard, 1984-1989 inclusive, based on observations of 107 individuals, 86 male and 21 female (see text).

of oak-fed larvae is orange to reddish brown, often with the spiracles and dorsolateral scoli surrounded by paler patches.

With respect to life history timing, Harris (1890: 404)writes: "The moth appears here [Massachusetts] from the 12th of June to the beginning of July, and then lays its eggs on the buttonwood [sycamore, *Liquidambar styracifolia*] tree. The caterpillars may be found upon this tree, grown to their full size, between the 20th of August and the end of September, during which time they descend from the trees to go into the ground." Phenologically, based on a sample of 107 individuals (86 male, 21 female) collected or observed

on Martha's Vineyard between 1982 and 1989, the
population is protandrous, and both males and
females peak at the end of July: 65% (56) of the males
were observed between 21 July and 1 August, and 71%
(15) of the females were observed between 25 July
and 1 August (Fig. 3). This flight season is consistent
with the collection dates of museum specimens from
the nearest known mainland historical records (e.g.
Cohasset, MA; Bristol, RI), has remained predictable
in the years since this study was conducted, and may
represent a more contracted flight season than that
reported in Tuskes *et al.* (1996) for northern *E. i.
imperialis*. Most individuals appeared at lights after
2200h, and individuals were observed coming to light
until 0400h.

Taken collectively, these observations hint at the
possibility that northern *E. imperialis* represents at
least one and possibly two biological entities distinct
from southern *imperialis*. It is noteworthy that Lemaire
(1988: 31) portrays the range of *E. i. pini* as crossing
the Appallachian divide to northern New England.
Although there exists a phenetic similarity of adult
New England specimens to individuals typical of *E. i.
pini* with respect to size and maculation, the diagnostic
characters of adult and larval *pini* (Tuskes *et al.*, 1996:
67, 68; Pls. 1, 7, & 8) do not appear in specimens from
New England. Historically, the superficially clinal
nature of variation in this complex has presented
obstacles to a clear understanding of what may be
taxonomically and biologically distinct natural entities.
Notwithstanding the perhaps controversial criteria on
which the retention of saturniid subspecific epithets
rely (Goldstein, 1997; but see Tuskes *et al.*, 1996 for
an alternative viewpoint), the similarities between
nominate *E. imperialis* and *E. i. pini* in wing maculation,
size, phenology, and especially host plant use are
relevant to the holobiology of this complex. It is
conceivable that the small size of *E. i. pini* and the New
England *E. i. imperialis* are related to the combination
of a short growing season and an apparently exclusive
association with pines at northern latitudes. I would
recognize *E. pini* as a full species and anticipate that
the northeastern, pine-feeding populations of *E.
imperialis* and those comprising *pini* will ultimately
be recognized as separate sister species. Since the
type locality of *Eacles imperialis* is in New York, I would
further anticipate that *nobilis* be resurrected.

Eacles imperialis on Martha's Vineyard: past and present

Jones and Kimball (1943), in their extensive
treatment of the Lepidoptera of Martha's Vineyard
and Nantucket Islands, described *E. imperialis* as

Figure 4. Current distribution of *E. imperialis* on Martha's
Vineyard as of 28 August, 2009. Courtesy Massachusetts
Natural Heritage & Endangered Species Program.
Westboro, MA.

occurring regularly on Martha's Vineyard, where it
persists and is widely distributed on both moraine
and outwash plain soils (Fig. 4). It is not known
from Nantucket, and virtually all mainland New
England specimens deposited in museum collections
I examined were taken during the first half of the
20th century, with only a few taken as late as the early
1950s. By all accounts, this species had essentially
declined dramatically in New England more than a
decade before Ferguson's (1971) publication, and
indeed was considered extirpated from Massachusetts
during the early drafting stages of the Massachusetts
Endangered Species Act (MESA; M.G.L. c. 131A and
regulations 321 CMR 10.00). It is currently listed as
"threatened" in Massachusetts.

The decline of *E. imperialis* in northeastern North
America is not unique, but rather consistent with
a well-known pattern of decline among saturniids
(Hessel, 1976; Ferguson, 1971; Frank, 1988; Schweitzer,
1988). In fact, the three most dramatic declines of
saturniids in New England have been ceratocampines:
E. imperialis, the royal walnut moth *Citheronia regalis*
(Fabricius), another of North America's most massive
saturniids, and the pine devil moth *C. sepulcralis* Grote
& Robinson, another barrens species that feeds on
pine and the type locality of which is Andover, MA.

Martha's Vineyard appears to have served as a
regional refugium for several species (e.g. *Actias
luna*) that remained extremely abundant on the
island while undergoing anecdotal declines—even
temporary ones—on the mainland. It is not at present
possible to single out any one of the various possible
causes for these declines; none are mutually exclusive.
Moreover the weak coincidence of the deployment

of metal halide street lights and pesticides several decades following the introduction of the tachinid fly *Compsilura concinnata* (Diptera: Tachinidae) in 1906 to combat gypsy moths and other pests (Howard & Fiske, 1911) makes parsing the relative importance of these factors difficult. In hindsight, it is not surprising that the sole New England population of *E. imperialis* to persist did so on an island that was not as heavily subjected to as heavy aerial deployment of pesticides or high-wattage metal halide streetlights, or to the intentional release of parasitoids, as the mainland.

Available data on the use of DDT and other pesticides, recorded on a per-county basis between 1948 and 1965, indicate that Dukes Co. (including Martha's Vineyard) was one of four counties sprayed only once during this period, and was subjected to less intensive treatment (as measured by total spray-acres) than any other county in the Commonwealth excepting Middlesex (Bewick, 1979, reproduced in Table 1). Martha's Vineyard is approximately 100 square miles, or 64,000 acres; its single documented pesticide treatment of 17,000 acres in 1956 is less intensive, for example, than the 31,071 acres sprayed on Nantucket, whose land mass is roughly half that of the Vineyard; and far less than the hundreds of thousands of acres of maritime barrens habitats in Plymouth and Barnstable counties routinely subjected to spraying before the use of DDT was discontinued.

Prior to the widespread deployment of DDT, the parasitoid fly *C. concinnata* had become well-established in New England, shortly after its 1906 introduction (Culver, 1919). Introduced to combat the gypsy moth

Lymantria dispar (L.), the browntail moth *Euproctis chrysorrhoea* (L.) and other pests, it quickly became apparent that this animal attacks a large and diverse assemblage of macrolepidopteran larvae (Webber & Schaffner, 1926; Arnauld, 1978). Recent observations by Boettner *et al.* (2000 and unpubl.) confirm the extraordinary impact of *C. concinnata* on several native saturniids on mainland New England and that the flies will attack *E. imperialis* caterpillars when presented with the opportunity. *Compsilura concinnata* is considered a stong candidate for playing a role in the demise of *E. imperialis* and other large moths on mainland New England (Boettner *et al.*, 2000); *Compsilura concinnata*'s occurrence on Martha's Vineyard has not been verified.

Regional variation and host plant use

Eacles imperialis feeds (and can certainly be reared) on a wide range of tree hosts (Ferguson, 1971; Stone, 1991; Tuskes *et al.*, 1996), to which it may be locally specialized, and the moth's range exceeds that of any recorded host plant species. Ferguson (1971) lists an impressive array of recorded hosts: "oak, hickory, walnut, sycamore, basswood, maple, honey locust, chokecherry, sumac, sweet gum, sassafras, elm, beech, hornbeam, birch, alder, pine, spruce, hemlock, cedar, cypress, and juniper." However, the degree to which a given population of *E. imperialis* is ever genuinely polyphagous in nature is not well studied. On Martha's Vineyard, *E. imperialis* appears to feed exclusively on pitch pine (*Pinus rigida*), a common tree associated with sandy, well-drained soils and barrens habitats. Pine-feeding is not unusual for *Eacles imperialis* elsewhere, nor is it restricted to the northernmost tier of the moth's range: Abbot and Smith (1797) observed pine-feeding in Georgia over two centuries ago, and pitch pine is a common host in the New Jersey pine barrens (D. F. Schweitzer, pers. comm.). All the recorded hosts of *E. i. pini* are conifers (Tuskes *et al.*, 1996), including jack pine (*Pinus banksiana*), which replaces *P. rigida* to the north and west of southern New England. From the perspective of consumption and digestion, conifer foliage represents a diet high in fiber, relatively low in water and nitrogen content, and possessed of allelochemical defenses such as monoterpenes stored in resin ducts (Raffa, 1991). The observation of localized conifer specialization on the part of *E. imperialis* is of interest both from the perspective of pine-herbivore biology and from that of the species' northeastern decline.

Host plant specificity among herbivorous insects in general and Lepidoptera in particular has been of broad interest to entomologists at least since the

Table 1. Massachusetts DDT spray history 1948-1965 (Reproduced from Bewick, 1979).

County	Total spray-acres	# Years treated	Avg. acres sprayed per treatment year
Plymouth	525,962	5	105,193
Hampshire, Hamden, Franklin	505,952	7	72,279
Barnstable	490,130	10	49,013
Worcester, Norfolk	374,905	2	187,453
Berkshire	324,765	7	46,395
Nantucket	31,071	1	NA
Essex	29,685	2	14,823
Bristol	18,496	1	NA
Dukes	17,000	1	NA
Middlesex	16,934	1	NA

works of Brues' (1920, 1924), which were followed by seminal ecological studies and reviews highlighting general patterns in the ecology and evolution of host use breadth (e.g. Ehrlich & Raven, 1964; Futuyma, 1976; Gilbert, 1979; Cates, 1980; Jermy, 1984). Adult oviposition cues play a critical role in host plant specialization (Wiklund, 1975), and variables such as host plant chemistry and architecture (Cates & Rhoades, 1977; Scriber & Feeny, 1979; Berenbaum, 1981; Bowers, 1983, 1984; Bernays, 1989), foliar water, nitrogen and fiber content (Scriber, 1977, 1979b; Mattson, 1980; Mattson & Scriber, 1987), and maternity (e.g. Mousseau & Dingle, 1991) effect lepidopteran digestive efficiency. Population genetic and phylogenetic data have been brought to bear on the evolution of host specialization and the role of host shifts in speciation (Berlocher, 1998), and the co-cladogenesis of insects and plants (Farrell & Mitter, 1990, 1998; Futuyma & McCafferty, 1990; Funk et al., 1995; Becerra, 1997; Farrell, 1998).

Studies of the ecophysiological roles of host plant growth form and seasonality (e.g. Tilton, 1977; James & Smith, 1978; Scriber, 1978) in mediating insect-plant associations are directly relevant to the evolution of pine feeding. From a nutritional perspective, folivores of trees and other woody plants represent a guild that must often contend with low nitrogen and water contents relative to graminivores or forb feeders, for example. Nitrogen is an important growth-limiting factor for many herbivores which may covary with water content (Mattson, 1980); low foliar water content can impede the growth and development of herbivores (Scriber, 1977) as well as a given herbivore's ability to utilize available nitrogen (Scriber, 1979a, b). These effects can be particularly severe with regard to the performance of tree feeders (Scriber, 1979b); since low nitrogen and water contents are typically associated with woody plants as opposed to forbs and grasses, folivores of trees often display low growth and utilization efficiencies (Scriber & Slansky, 1981).

I pursued a line of investigation towards better understanding host plant use in the relictual population of this moth, specifically the question of whether the apparent confinement to pines is nutritionally imposed or the result of some unknown non-nutrionally based or abiotic factor. This endeavor comprised laboratory-based experiments focusing on the role of food plant in influencing larval growth and development. Given the considerable range-wide variation in host use among geographically delimited populations of E. imperialis, the notion that such local specialization may have been accompanied by physiological adaptation is of interest from the perspective of understanding host shifts, regardless

of whether they accompany speciation per se.

MATERIALS AND METHODS

Five treatments from four species of host plants were chosen on the basis of recorded use by E. imperialis, availability and, in the case of pitch pine, comparability between material from wild populations known to be used by E. imperialis and arboretum-raised material. Pitch pine is the only known host of E. imperialis on Martha's Vineyard (personal observations of both larvae and wild oviposition behavior of adult females), and was reported as the favored larval host of other Massachusetts E. imperialis (Eliot & Soulé, 1902). The jack pine P. banksiana was chosen because it is associated with E. imperialis pini (Michener, 1950; M. C. Nielsen, pers. comm.; B. Scholtens, pers. comm.), comprising the northernmost named subspecies of E. imperialis and the only other regional populations associated exclusively with conifers. Jack pine may be considered an ecological analog of pitch pine, in that it replaces the latter in habitats to the north and west characterized by granitic soils that, like maritime pitch pine-scrub oak barrens, are sandy, well-drained, and acidic soils (Little, 1979; Schweitzer & Rawinsky, 1988). M. C. Nielsen (pers. comm.) reports that E. i. pini appears most commonly in association with jack pine on Grayling soils. With the exception of tiny remnant stands such as that at West Rock, New Haven, CT, the post oak Q. stellata is represented in New England primarily as a disjunct population on Martha's Vineyard. The nearest large stands of Q. stellata occur on Long Island, N. Y. and in the New Jersey pine barrens, which also hosts the largest northeastern population of E. imperialis. The black walnut J. nigra was chosen because it is a recorded host of E. imperialis, yet does not occur regularly on Martha's Vineyard. Food plant material was harvested every five days from the Felix Neck Wildlife Sanctuary, Edgartown, MA (pitch pine and post oak) and the Arnold Arboretum, Jamaica Plain, MA (pitch pine, jack pine, and black walnut). Upon cutting, plant material was placed in water pics and maintained at 40°F until used.

Foliage fitted with water pics was placed in rearing containers, the supply of fresh food maintained, and the container cleaned of frass every five days. Since foliar water and nitrogen concentrations have been demonstrated to decrease with leaf age (Axelsson & Agren, 1979; Slansky & Scriber, 1985), it was therefore important to be as consistent as possible when selecting plant material so that foliage treatments of wildly disparate ages were not lumped under the same heading.

Gravid females from Martha's Vineyard were collected in 1988 and 1989 at light and placed in paper bags for oviposition. Ova were harvested and segregated according to parent, then maintained in 4" diameter petri dishes under constant conditions of light and temperature (per day, 14 hours light at 25°C and 10 hours darkness at 20°C). The 1988 livestock came from four females taken between 31 July and 5 August at three different sites on Martha's Vineyard: Cedar Tree Neck, West Tisbury (4 August, 110 ova); Makonikey, West Tisbury (3 and 5 August, 155 and 78 ova); and Pennywise Path, Edgartown (31 July, 107 ova).

During the first (1988) season's experiments, ova were selectively cooled at 50°F for up to four days to synchronize hatching. Larvae from each clutch were weighed upon hatching, placed on each of five of the food plant cohorts, and weighed every five days (116 hours) through day 15 in all cases and day 20 when possible. Larvae were reared individually, first in 4.0" petri dishes for their first five days, and then in plastic containers 4.5" in diameter and 3.5" in height. Humidity was maintained using 1" x 2" cut sections of paper towels secured to the container lid and moistened twice every five days. All larvae were maintained under constant conditions of temperature and lighting as described above. Since leaves that remain attached to the stem are generally less apt to lose water than if they are cut (Schroeder, 1984), food plant freshness was maintained by placing plant sprigs (or petioles, in the case of *J. nigra*) in water pics situated in larval rearing containers.

Weights of surviving larvae from different clutches and on different host plants were natural log-transformed and compared (2-way ANOVA) for each weighing interval through Day 15. The influence of food plant treatment was further analyzed (1-way ANOVA) by lumping all surviving larvae of a given food plant treatment and age regardless of parentage.

In 1989 these experiments were repeated in part and with several modifications, using ova from seven females collected between 26 and 28 July from three sites on Martha's Vineyard: Lobsterville, Aquinnah (26 July, 178 ova); Cedar Tree Neck, West Tisbury (three females, all 27 July; 55, 125, and 169 ova); and Makonikey, West Tisbury (three females, 26, 27, and 28 July; 178, 50, and 104 ova). The 1989 work focused exclusively on two food plants taken from current *E. imperialis* habitat (*P. rigida*, the native host, and *Q. stellata*, with all plant material taken from Felix Neck Wildlife Sanctuary, Edgartown, MA. Eggs were not cooled to synchronize hatching, and in order to minimize handling of young larvae, all hatchling caterpillars were started not in petri dishes but in the

larger plastic containers. Given observations that hatchling larvae lost weight to desiccation quickly, care was taken to ensure that every larva was weighed and placed on the appropriate food plant immediately upon hatching. To maintain humidity, I used 1" x 1" x 2" sponges, washed at each weighing instead of paper towel sections. The sponge holds more water and for a longer period of time and does not require additional moistening between weightings. All sponge blocks were washed repeatedly prior to use to clear them of chemical additives, and thoroughly cleaned of larval frass at each weighing to avoid mold. Food plants were maintained as in 1988 at 40°F, misted with distilled water and given refreshed water pics every 24 hours. Feedings were made as close to identical as possible; all the feedings for a given weighing interval and food plant species consisted of material cut from a single tree. Sample sizes were increased to fifteen larvae per female per food plant treatment initially, for 104 larvae in total on each food plant. Color morph and instar were noted at each weighing and larvae were reared to pupation, sexed and weighed again. Weights were analyzed as described through day 20 for all larvae and pupae. Since *E. imperialis* is a sexually dimorphic species, male and female pupae were compared separately (1-way ANOVA) for each food plant cohort. Weights upon hatching were compared independent of a food plant effect (one-way ANOVA) to evaluate bias in assigning larvae to food plants. There was not a large enough sample size per sex per clutch to retrieve any significant data regarding a maternal effect on pupal weight. However, all pupal weights representing each sex were lumped for each food plant in order to test for a food plant effect via one-way ANOVA.

The gravimetric assessment of digestive and growth indices involved forty offspring of a single female on four of the 1988 food plant treatments: both wild and arboretum-grown *P. rigida*, arboretum-grown *P. banksiana*, and wild *Q. stellata*. Low survivorship on *J. nigra* precluded there being enough data to analyze. These indices were: relative growth rate (RGR); relative consumption rate (RCR); approximate digestibility (AD); efficiency of conversion of ingested food to biomass (ECI); and efficiency of conversion of digested food to biomass (ECD). The experimental regime employed here involved monitoring the food uptake and utilization during the course of a single instar, from the beginning of the third to the beginning of the fourth instar. All vegetative material used in these experiments consisted of pre-weighed individual leaves or sprigs; unconsumed food and frass was dried at 95°F and re-weighed. Control samples of plant material for each feeding were also weighed,

dried, and re-weighed for the purpose of calculating conversion factors. Larvae were weighed at the beginning and end of the experiment, then frozen, dried, and re-weighed to determine the dry weight gained by each larva. Each larva thus provided its own conversion factor, its final dry weight treated as a percentage of its final fresh weight and used to estimate initial dry weight. Based on these weights of plant and larval material, the five food plant utilization measures were determined following Waldbauer (1968). For each larva used in the calculation of utilization indices, the dried control food plant material was ground and analyzed for percent-nitrogen using a Kjeltec nitrogen analysis system. Mean digestive indices were compared via one-way ANOVA.

The gravimetric assessment of performance has been reviewed and critiqued numerous times since its introduction (Scriber & Slansky, 1981; Schroeder, 1984; Agren & Axelsson, 1979; Bowers *et al.*, 1991), and a substantial body of literature has been devoted to evaluating the various sources of error associated with this method. A significant methodological source of error in the calculation of such nutritional indices derives from the indirect calculation of the dry weight of plant material and of the initial dry weight of the larva (Bowers *et al.*,1991). Since the host plants used differ in megaphyll morphology, achieving similarity between treatment and controls is difficult to standardize. This necessitated frequent feeding of fresh plant material in order to minimize the differential effects of desiccation on digestibility. For each feeding of *Q. stellata*, a single leaf was bisected, half used to determine the dry weight conversion factor. Conversion factors for *P. rigida* involved the use of individual needles excised from sheaths: for each needle-bearing sheath, a single needle was removed for immediate drying while the others were used for feeding. This method has the dual advantages of providing as accurate a control as possible, since all needles within a given sheath are the same age and size, and of minimizing damage to both treatment and control, since the sheath can be removed from its enclosed needles without tearing or severing significant mesophyll tissue.

Preliminary work showed that the short needles of *P. banksiana*, which occur in pairs, were more vulnerable to desiccation than those of *P. rigida*. To offset desiccation, single needles were therefore retained intact within bisected sheaths, the dry weight of the inedible sheath later subtracted from the estimated dry weight of the initial feeding prior to calculation of fresh weight/dry weight conversion factors.

RESULTS

Food plant and maternal effects on growth

Larval growth varied considerably across the 1988 food plant treatments. The (1988) data indicated that *E. imperialis* larvae grew more slowly at first on the deciduous plants than conifers, with growth most markedly retarded among the larvae fed *J. nigra* (Table 2, Fig. 5). Based on weight, larvae responded best to the diet of arboretum-grown *P. banksiana*, followed by that of arboretum-grown *P. rigida*, wild *Q. stellata* and finally wild *P. rigida*. However, for a period between the second and third weightings (days 5 and 10), the growth of larvae fed *Q. stellata* surpassed that of the other food plant cohorts. Most larvae fed arboretum-grown jack pine and pitch pine weighed more at Day 20 than those given other food plants. ANOVA indicated significant food plant as well as maternal effects on larval growth (Table 3), the latter far less marked than the former.

Larvae in the 1989 follow-up growth experiments, conducted under modified conditions where foliar water was more rigorously ensured, consistently gained biomass and molted earlier when fed post oak than when fed pitch pine, unambiguously demonstrating enhanced performance of *E. imperialis* on wild *Q. stellata* relative to wild *P. rigida* based on larval growth and pupal weight (Fig. 6; Tables 4, 5), again with significant differences attributable both to food plant and to maternity in each of the host plant treatments (Table 6; Figs. 7, 8).

The variation in larval growth attributable to maternal effects was, as in 1988 (Table 3), small relative
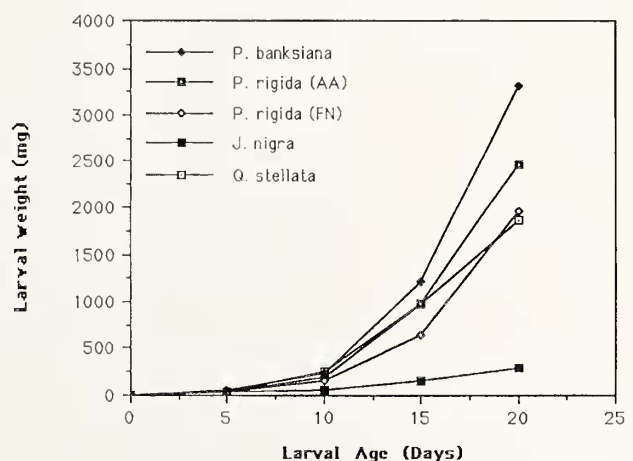

Figure 5. Fresh weight (mg) of *E. imperialis* on five food plant treatments taken at 5-day intervals, 1988. *Cf.* Table 2.

Table 2. Weights (mg) of larvae reared on five food-plant treatments, 1988. *x* = mean; se = standard error; *N* = sample size; AA = foliage used from Arnold Arboretum, Jamaica Plain, MA; FN = foliage used from Felix Neck Wildlife Sanctuary, Edgartown, MA. Cf. Fig. 5.

Age (days)	*Pinus rigida* (FN) x(se)	*Pinus rigida* (AA) x(se)	*Quercus stellata* (FN) x(se)	*Pinus banksiana* (AA) x(se)	*Juglans nigra* (AA) x(se)
0	9.384 (0.083) N=19	8.9 (0.081) N=19	9.47 (0.0653) N=23	7.632 (0.069) N=19	8.411 (0.083) N=19
5	43.947 (0.213) N=19	45.968 (0.21) N=19	40.335 (0.179) N=23	59.058 (0.311) N=19	34.211 (0.191) N=19
10	157.789 (.495) N=19	203.158 (0.45) N=19	246 (0.562) N=23	243.342 (0.556) N=19	68.618 (0.409) N=17
15	652.829 (1.279) N=14	988.174 (0.865) N=19	973.099 (1.068) N=19	1219.421 (1.185) N=19	160.769 (0.851) N=13
20	1964.592 (2.479) N=14	2471.57 (2.54) N=10	1867.557 (3.629) N=7	3320.9 (1.869) N=14	296.788 (1.783) N=8

Table 3. Analysis of variation due to food-plant and maternal effects on larval growth, 1988. NA = not applicable.

	Variation due to foodplant			Variation due to maternal effects		
Larval age (days)	DF	F-ratio	P-value	DF	F-ratio	P-value
0	4	NA	NA	3	1.08	0.362
5	4	3.988	0.005	3	6.297	0.001
10	4	22.329	<.001	3	6.259	0.001
15	4	55.356	<.001	3	4.393	0.007

Table 4. Weights (mg) of *E. imperialis* reared on *P. rigida* and *Q. stellata* at ages 0 through 20 days, 1989, followed by pupal weights for males and females. Range refers to mean values for offspring of a given female (not applicable for pupal weights). Cf. Fig. 6.

	Pinus rigida		*Quercus stellata*	
Larval age (days)	x(se)	Range	x(se)	Range
0	10.221 (0.013) N=104	8.334-11.727	10.315 (0.014) N=104	8.531-12.358
5	47.803 (0.035) N=104	41.508-58.789	59.227 (0.044) N=100	53.389-66.627
10	315.042 (0.118) N=102	229.862-468.191	555.959 (0.213) N=92	383.782-647.46
15	1516.205 (0.268) N=96	1161.357-2013.193	2195.288 (0.328) N=86	1516.931-2711.417
20	3561.943 (0.349) N=93	3007.108-4226.031	4484.786 (0.387) N=87	3517.45-5599.417
Male pupal weight (mg)	3719.304 (0.936) N=26	NA	4751.297 (0.786) N=29	NA
Female pupal weight (mg)	4473.514 (1.199) N=22	NA	5705.4 (1.277) N=22	NA

Table 5. Summary and analysis of development of *E. imperialis* in therms of instar on *P. rigida* and *Q. stellata*.

	Day 5			Day 10		Day 15		Day 20	
Instar	1	2	2	3	3	4	4	5
# Pine-fed larvae	24	80	13	89	8	88	28	65
# Oak-fed larvae	6	96	2	90	1	91	12	73
G-value	13		9		6		7	
P-value	<.001		<.005		<.025		<.025	

Table 6. Analysis of food-plant and maternal effects on larval growth, 1989. NA = not applicable; NS = insufficient data.

	Variation due to foodplant			Variation due to maternal effects		
Larval age (days)	DF	F-ratio	P-value	DF	F-ratio	P-value
0	NA	NA	NA	6	15.547	<.001
5	1	26.194	<.001	6	3.643	0.002
10	1	55.112	<.001	6	6.176	<.001
15	1	25.382	<.001	6	6.507	<.001
20	1	24.34	<.001	6	5.593	<.001
Male pupa	1	40.049	<.001	NS	NS	NS
Female pupa	1	28.115	<.001	NS	NS	NS

Table 7. Summary and analysis of nutritional indices obtained on four food-plant treatments. AA = foliage used from Arnold Arboretum, Jamaica Plain, MA; FN = foliage used from Felix Neck Wildlife Sanctuary, Edgartown, MA.

Nutritional index	*Pinus rigida* (FN)	*Pinus banksiana*	*Pinus rigida* (AA)	*Quercus stellata*	One-way ANOVA F-ratio	P-value
	x(se)	x(se)	x(se)	x(se)		
AD	31.09 (0.6) $N=4$	31.64 (0.431) $N=7$	28.78 (0.259) $N=9$	26.5 (0.283) $N=7$	0.898	0.457
ECD	32.16 (0.714) $N=4$	39.38 (0.647) $N=7$	41.96 (0.331) $N=9$	46.22 (0.43) $N=7$	1.056	0.387
ECI	15.01 (0.304) $N=4$	16.35 (0.197) $N=7$	18.08 (0.126) $N=9$	18.48 (0.208) $N=7$	4.778	0.01
RGR	0.205 (0.04) $N=4$	0.244 (0.021) $N=7$	0.251 (0.022) $N=9$	0.264 (0.032) $N=7$	2.157	0.121
RCR	0.473 (0.072) $N=4$	0.49 (0.04) $N=7$	0.414 (0.02) $N=9$	0.425 (0.04) $N=7$	2.178	0.118
%N	5.83 (0.052) $N=8$	6.79 (0.086) $N=8$	6.84 (0.048) $N=8$	8.07 (0.091) $N=8$	48.973	<.001

to that attributable to host plant. One trend is that of the consistent relative growth of offspring of several females; mean larval weights for each of four females on post oak were more massive than on pitch pine by Day 5, remaining so at every consecutive weighting through Day 20. The offspring of each of the four females grew, relative to one another, in exactly the same order on oak and pine, with the offspring of female 5 outdistancing those of females 6, 7, and 2, respectively (Figs. 7, 8). This trend implies that there
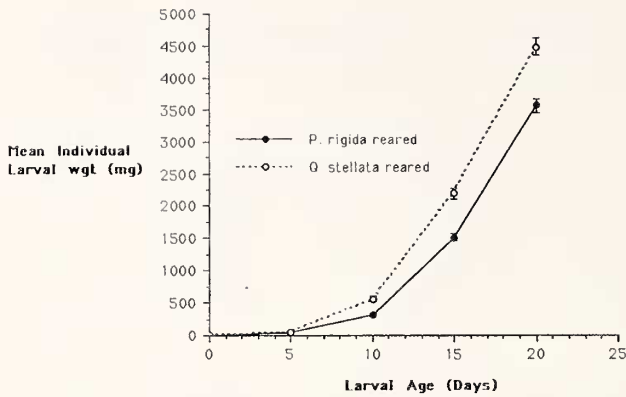
Figure 6. Fresh weight (mg) of *E. imperialis* on pitch pine *P. rigida* and post oak *Q. stellata*, 1989. Cf. Table 4.
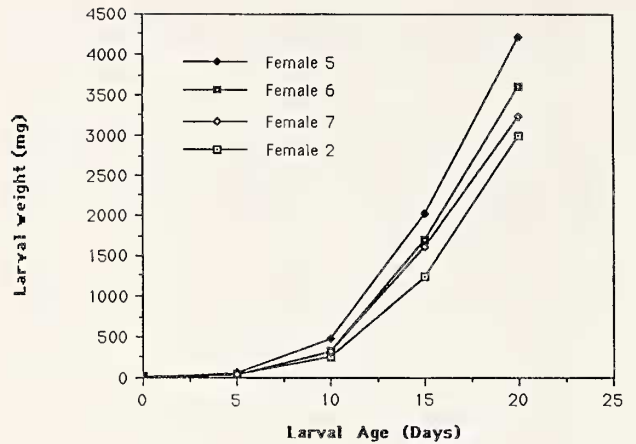

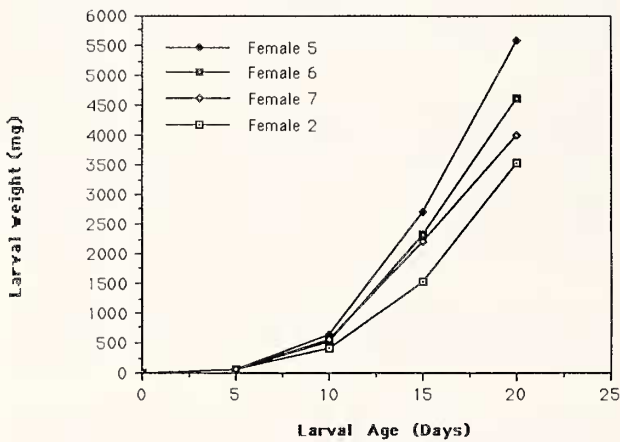**Figure 7.** Fresh weight (mg) of oak-fed offspring from four female *E. imperialis*, 1989.

Figure 8. Fresh weight (mg) of pine-fed offspring of four females of *E. imperialis*, 1989.

exists little trade-off in relative efficiency from oak to pine. That is, a larva well-equipped to utilize pine relative to another larva may be just as relatively well equipped to utilize oak. This explanation is consistent with the fact that no statistically significant interaction exists between the parental effect and the food plant effect. Significant differences appeared among mean weights of larvae from different clutches at each weighing and among mean weights of hatchling larvae, but these relative differences did not persist as such at subsequent weighings. Since there were no significant differences between mean weights of hatchling larvae given different food-plant treatments, these results can not be attributed to bias in the initial separation of larvae into treatment cohorts.

A comparison of the numbers of larvae that had achieved a given instar by a given age revealed the following: significantly more of the oak-fed larvae than the pine-fed larvae molted to second instar by Day 5 (DF=1, G=12.996), third instar by Day 10 (G=8.502), fourth instar by Day 15 (G=6.162), and fifth instar by Day 20 (G=6.688). Additionally, mean male and female pupal weights were significantly higher for oak-fed larvae (4751.297 mg and 5705.4 mg, respectively) than for pine-fed larvae (3119.304 mg and 4473.514 mg, respectively).

In both years the number of larvae exhibiting the green color morph was higher for the pine-fed cohort than the oak-fed cohort. Exactly 50% (52 of 104) of all the 1989 larvae reared on pine exhibited green coloration; most of these turned green at the second molt (beginning of the third instar), and seven reverted to brown at subsequent molts, five at the third and two at the fourth. Of the 52 green larvae from both 1989 food plant treatments, only four had been reared on oak. As many as 13 of 15 and as few as 5 of 15 offspring of a given female fed pitch pine were green. Almost all larvae reared on oak exhibited a lighter brown or reddish body color.

Nutritional indices

Nutritional indices, calculated exclusively during the third instar, corroborated enhanced growth rate and efficiency on oak relative to pine, as did the higher pupal weights among oak-fed versus pine-fed larvae (Table 7). The efficiency of conversion of ingested food (ECD), the efficiency of conversion of digested food (ECI), and the relative growth rate (RGR) were positively correlated with foliar nitrogen and

water content across food plants; the approximate digestibility (AD) and the relative consumption rate (RCR) were not. The only significant differences, however, were among the ECI and percent nitrogen values. The foliage of wild grown post oak and arboretum grown pitch pine contained significantly more nitrogen and water than corresponding amounts of wild pitch pine and arboretum-grown jack pine, and these numbers were paralleled by larval ECIs. (Table 7).

DISCUSSION

The life history constraints of host specialization have been an important focus within the study of herbivore evolution. It has been hypothesized that the limits imposed by a contraction in the spectrum of potential host species are offset by an enhanced efficiency with which an herbivore utilizes that narrower host range (Brues, 1924; House, 1962; Emlen, 1973; Gilbert, 1979). The validity of this "feeding specialization hypothesis" is central to our understanding of evolved herbivory (Slansky & Scriber, 1985). Not only have consistent patterns of higher utilization efficiencies among monophagous versus polyphagous or oligophagous herbivores failed to be demonstrated, but Scriber and Feeny (1979) have contended that host plant chemistry is responsible for most of the variation seen in larval performance. That is to say the "costs" of specialization have not been well-defined or demonstrated in a broad sense because the axes along which organisms specialize may or may not intersect. It has become increasingly clear that in order to effect proper experimental and analytical procedures to test the feeding specialization hypothesis as a general paradigm, one must recognize a range of organism-specific variables, from elements in plant foliage that affect herbivore development to life history manifestations of constraints imposed by the host plant. These variables defy simple patterns, being too numerous and interdependent for their roles to be parsed except very broadly (Gaston & Reavey, 1989). Scriber (1983) suggested that one reason for our relative lack of understanding derives from the paucity of studies narrowly focused on groups of taxonomically and ecologically similar organisms. To these I would add studies of ecologically similar but phylogenetically independent and phylogenetically well understood groups.

Notwithstanding the predictable effects of nutrient rich foliage among arboretum-grown plants relative to wild foliage, the growth rates and efficiencies of consumption and digestion of oak versus the wild pine host suggest that, nutritionally, New England imperial moth caterpillars do not require pitch pine alone in order to survive. At the same time, *E. imperialis* may be adapted or pre-adapted physiologically to conifers. Conifer feeding on the part of herbivorous insects represents a nutritional dynamic different from deciduous leaf feeding. Pitch pine, in particular, is a complicated fire-adapted plant, and perhaps a more relevant comparison than that between larval performance on arboretum-grown, well-fertilized plants and performance on native hosts of disjunct moth populations might be undertaken between geographically disparate populations on the wild northern conifer hosts and among different age cohorts of pitch pine foliage growth in viable habitats of *E. imperialis*. That said, differential patterns in nutritional content between evergreen and deciduous trees have been demonstrated (Miller & Stoner, 1979), with evergreen foliage having generally lower nutrient contents. Pines and other conifers typically contain less foliar nitrogen than deciduous angiosperms under similar conditions of growth and development (Bidwell & Durzon, 1975; Slansky & Scriber, 1985), and wild pitch pine from barrens and typically nutrient-poor (Forman, 1979; Schweitzer & Rawinski, 1988). Folivores of nutrient-poor, woody plants tend to show greater breadth of dietary tolerance (i.e. be more polyphagous) than those on highly nutritious foliage (Mattson & Scriber, 1987). Mattson and Scriber (1987) cite Holloway and Hebert (1979) who found that conifer-feeding Lepidoptera "are less specific in host plant choice than species feeding on angiosperms." The data presented in this study are consistent with this claim in that the larvae of *E. imperialis* are capable of sustained development on different hosts. Both the published host records of *E. imperialis* and the results of this study support the contention that this species, including populations functionally restricted to pine, can metabolize a broad range of potential if not realized host plants.

Large body size is also considered an advantage when feeding on low-nutrient diets (Wasserman & Mitter, 1978; Peters, 1983; Mattson & Scriber, 1987), such as pines or late-season tree foliage. In fact, tree-feeding lepidopteran species active late in the growing season tend to be large (Mattson, 1980; Niemela *et al.*, 1981), as would be expected especially for those in which the adults do not feed (Slansky & Scriber, 1985) such as *E. imperialis*. There may also exist such a trend for folivores of evergreen versus deciduous plants. Opler (1978) noted that leafminers feeding on evergreen oak species tended to be larger than those on deciduous species. Although phylogenetic data were not yet available to evaluate the evolution of size in a cladistic framework, numerous authors

have observed phylogenetically biased patterns in lepidopteran size associated with host plant use and life history (Mattson, 1977; Wasserman & Mitter, 1978; Niemela *et al.*, 1981; Hayes, 1983; Gaston & Reavey, 1989), and although adaptive speculation is frivolous, it is worth noting that *E. imperialis*, the most massive saturniid extant in New England, is also the latest feeding saturniid in the region, active as larvae as late as October. By this time many of the host plants utilized further south, where the flight season of *E. imperialis* is more protracted, are senescent or nearly so northward, potentially accounting in part for the more strict association with conifers northward.

In contrast to pitch pine, wild grown post oak contained significantly higher amounts of nitrogen than even arboretum grown pitch pine, even though ECI's were not significantly different for larvae fed the two food plants. This implies either more efficient nitrogen utilization of pitch pine versus post oak on the part of *Eacles* or simply that oak contains more nitrogen than *Eacles* larvae can effectively metabolize. Despite the fact that the only two plant cohorts for which nitrogen content was not significantly different were the two arboretum-grown pines, the mean ECI was significantly higher for larvae on arboretum-grown pitch pine than for those on jack pine; both were significantly higher than for wild pitch pine. The mean ECI for arboretum-grown pitch pine was comparable to (i.e. not significantly different from) that of Martha's Vineyard post oak, on which larvae had the highest ECIs, and which supported a significantly higher nitrogen content (in fact the highest of all food plants measured). Taken collectively, these results suggest a potential physiological adaptation to pine-feeding in general, and pitch feeding specifically on the part of northern *E. imperialis*.

The results presented here go to show that simply because a particular food plant species meets an herbivorous organism's nutritional requirements and the organism is physiologically capable of growth and development on that food is not an indication that it is an actual, realized host in nature. There might be any of a number of possible explanations for the fact that Massachusetts *E. imperialis* larvae appear to grow faster and more efficiently on a non-utilized host (*Q. stellata*) than on the native host (*P. rigida*). Chemical oviposition cues such as terpenes specific to conifers, selective predation of larvae on one host versus another, abiotic habitat requirements of soil pupation, and even simple availability may all play a role in the restriction of northern *E. imperialis* to conifers. For example, I observed late instars of wild-reared larvae placed on *Q. stellata* undergo heavy predation by vespid wasps (*Vespa vulgaris*; pers. obs.)

relative to those reared *in situ* on *P. rigida*. The frass of oak-feeding larvae is less dry and more prone to mold than that of pine-feeding larvae, and may serve to attract predators.

The restriction of *Eacles imperialis* to the common pitch pine on Martha's Vineyard is of interest from the standpoint of conservation as well as evolutionary ecology. *Eacles imperialis* is one of 24 regionally threatened moth species occurring on Martha's Vineyard protected under the Massachusetts Endangered Species Act (MESA; M.G.L. c. 131A and regulations 321 CMR 10.00), not including at least one additional species, *Datana contracta* (Notodontidae) that appears to have been impacted severely on mainland southern New England and may be locally extirpated. As thorough an understanding as possible of why species such as these have declined—and what they require to persist—is a mission-critical prerequisite to any reintroduction and restoration effort. As conservationists consider potential sites at which to reintroduce and restore this species, we must weigh a variety of considerations, among them suitability of habitat, availability of host plant, probability of success, verifiability of historical occurrence, and legal logistics.

Biologically, the most obvious candidate sites, those showing the greatest promise for success, are barrens habitats on Cape Cod and in Plymouth County and on Nantucket Island. Ironically, historical records of *E. imperialis* from Cape Cod are lacking, and the conspicuous absence of this moth and its near relatives from Nantucket has long been noted: Jones and Kimball (1943) made the observation that although four species of ceratocampine saturniids occur on Martha's Vineyard, none were known at the time of that writing from Nantucket. Jones and Kimball speculated that such heavy bodied moths found it difficult to distribute across water barriers. As was the case during Jones and Kimball's time, four species of Ceratocampinae (*E. imperialis*, *Anisota senatoria*, *A. stigma*, and *A. virginiensis*) persist in numbers on Martha's Vineyard. *Anisota stigma*, at one point listed under the Massachusetts Endangered Species Act, occurs less ubiquitously on mainland New England than on Martha's Vineyard (Mello *et al.*, 1999). However, this species has apparently colonized Nantucket (K. Coombs-Beattie, pers. comm.; Goldstein, 1997), where it now occurs commonly, possibly obviating the argument that all ceratocampines have difficulty crossing water barriers.

Although Jones and Kimball did not discuss the historical ecology or land use history *per se* of either island, the possible role of habitat destruction and fragmentation of barrens habitats must be considered.

There can be little debate that viable habitat persists at mainland barrens sites, including the extensive maritime barrens in Plymouth County at Myles Standish State Forest (approx. 16,000 acres) and at the Massachusetts Military Reservation (roughly 15,000 acres), as well the 2,000 acre inland barrens at Montague Plain, Franklin Co., MA and on Nantucket Island. Jones and Kimball's (1943) observation that ceratocampines were absent from Nantucket during the 20th century of course begs the question of whether they were ever there. The land use history of Nantucket, like that of Martha's Vineyard, involved significant alteration and conversion of forested and shrubland habitats for the purposes of agriculture (Dunwiddie, 1992). Although both Martha's Vineyard and Nantucket were part of an extensive coastal plain as recently as 10,000 years ago, Nantucket was almost completely denuded of forest during the Revolutionary War, which no doubt had an impact on the lepidopteran fauna. It may be observed that, in addition to the ceratocampines, other groups of forest tree Lepidoptera are depauperate on that island relative to Martha's Vineyard. There is a marked contrast, for example, between the islandic faunas of Limacodidae: whereas nine species of limacodids (*Euclea delphinii, Isa textula, Phobetron pitchecium, Prolimacodes badia, Apoda biguttata, Lithacodes fasciola, Packardia elegans, P. geminata, Torticidia flexuosa*) occur regularly on Martha's Vineyard, only two (*E. delphinii* and *L. fasciola*) were recorded on Nantucket by Jones and Kimball (1943: 123-125). Jones and Kimball's data also suggest a comparative dearth of leaf litter feeding deltoid noctuids on Nantucket relative to Martha's Vineyard, which would be expected following systemic deforestation.

Pitch pine, however, is now an extremely common plant on Nantucket and, ironically, it is conceivable that the introduced tachinid *C. concinnata*, to be verified from the island of Martha's Vineyard or Nantucket, may prevent the re-establishment of *E. imperialis* on mainland New England. It has yet to be determined whether or not the introduced parasitoid *C. concinnata* poses a barrier to recolonizing the mainland, whether or not the fly's absence on Martha's Vineyard is, if not an artifact of under-sampling, a reason for *Eacles*' persistence there.

Acknowledgements

Literature Cited

Abbot, J. & J. E. Smith. 1797. The natural history of the rarer lepidopterous insects of Georgia. 2 vols. London: printed by T. Bensley for J. Edwards.

Arnauld, P. H., Jr. 1978. A host-parasite catalog of North American Tachinidae (Diptera). USDA, Science and Education Administration, Washington, D. C. publication 1319.

Agren & Axelsson. 1979. Energy budgets do balance. Oecologia 42: 375-376.

Becerra, J. X. 1997. Insects on plants: macroevolutionary chemical trends in host use. Science 276: 253-256.

Berenbaum, M. 1981. Patterns of furanocoumarin distribution and insect herbivory in the Umbelliferae: plant chemistry and community structure. Ecology 62: 1254-1266.

Berlocher, S. H. 1998. Can sympatric speciation be proven from biogeographic and phylogenetic evidence? Pp. 3-15. *In*: D. J. Howard and S. H. Berlocher (eds), Endless forms: species and speciation. New York, NY: Oxford University Press.

Bernays, E. A. 1989. Host range in phytophagous insects: the potential role of generalist predators. Evolutionary Ecology 3: 299-311.

Bewick, J. A. 1979. Gypsy moth control project report. Massachusetts Executive Office of Environmental Affairs. Boston, MA.

Bidwell, R. G. S. & D. J. Durzon. 1975. Some recent aspects of nitrogen metabolism. Pp. 152-155. *In*: P. J. Davies (ed.), Historical and current aspects of plant physiology: a symposium honoring F. C. Stewart. State College of Agricultural and Life Sciences, New York.

Boettner, C. J., J. S. Elkinton, & C. G. Boettner. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conservation Biology 14(6): 1798-1806.

Bowers, M. D. 1983. Iridoid glycosides and larval hostplant specificity in checkerspot butterflies (*Euphydryas*, Nymphalidae). J. Chem. Ecol. 9: 475-493.

Bowers, M. D. 1984. Iridoid glycosides and hostplant specificity in larvae of the buckeye butterfly, *Junonia coenia* (Nymphalidae). J. Chem. Ecol. 10: 1567-1577.

Bowers, M. D., N. E. Stamp, & E. D. Fajer. 1991. Factors affecting calculation of nutritional indices for foliage feeding insects: an experimental approach. Entomologia Experimentalis &

Applicada 61: 101-116.

Brues, C. T. 1920. The selection of food-plants by insects, with special reference to lepidopterous larvae. Am. Nat. 54: 313-332.

Brues, C. T. 1924. The specificity of foodplants in the evolution of phytophagous insects. Am. Nat. 58: 127-144.

Cates, R. G. 1980. Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. Oecologia (Berl.) 46: 22-31.

Cates, R. G. & D. F. Rhoades. 1977. Patterns in the production of anti-herbivore chemical defenses in plant communities. Biochem. Syst. Ecol. 5: 185-193.

Covell, C. V. 1984. A field guide to the moths of Eastern North America. Boston: Houghton Mifflin, Co.

Culver, J. J. 1919. A study of *Compsilura concinnata*, an imported tachinid parasite of the gipsy moth and the brown-tail moth. United States Department of Agriculture, Bulletin 766.

Dunwiddie, P. W. 1992. Changing landscapes: a pictorial field guide to a century of change on Nantucket. Privately published.

Ehrlich, P. R. & P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586-608.

Eliot, I. M. & C. G. Soulé. 1902. Caterpillars and their moths. New York: The Century Co.

Emlen, J. M. 1973. Feeding ecology. Pp. 157-185. *In*: Ecology: an evolutionary approach. Reading, MA: Addison-Wesley.

Farrell, B. D. 1998. "Inordinate fondness" explained: why are there so many beetles? Science 281: 555-559.

Farrell, B. D. & C. Mitter. 1990. Phylogenetics of insect/plant interactions: have *Phyllobrotica* leaf beetles (Chrysomelidae) and the Lamiales diversified in parallel? Evolution 44: 1389-1403.

Farrell, B. D. & C. Mitter. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? Biol. J. Linn. Soc. 63: 553-577.

Farquhar, D. W. 1934. The Lepidoptera of New England. PhD dissertation, Harvard University.

Ferguson, D. C. 1971. The moths of North America, Fascicle 20.2A Bombycoidea: Saturniidae (Part). London: Curwen Press.

Forman, R. T. T (ed.). 1979. Pine barrens: ecosystem and landscape. New York: Academic Press.

Frank, K. D. 1988. Impact of outdoor lighting on moths: an asessment. Journal of the Lepidopterists' Society 42: 63-93.

Funk, , D. J., D. J. Futuyma, G. Orti, & A. Meyer. 1995. A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. Evolution 49: 1008-1017.

Futuyma, D. J. 1976. Foodplant specialization and environmental predictability in Lepidoptera. Am. Nat. 110: 285-292.

Futuyma, D. J. & S. S. McCafferty. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera: Chrysomelidae). Evolution 44: 1885-1913.

Gaston, K. J. & D. Reavey. 1989. Patterns in the life histories and feeding strategies of British macrolepidoptera. Biol. J. Linn. Soc. 37: 367-381.

Gilbert, L. E. 1979. Development of theory in the analysis of insect-plant interactions, pp. 117-154. *In*: D. J. Horn, G. S. Stairs, and R. D. Mitchell (eds.), Analysis of Ecological Systems. Columbus: Ohio State University Press.

Goldstein, P. Z. 1991. Investigation of the natural history and nutritional ecology of a remnant population of *Eacles imperialis* Drury on Martha's Vineyard Island, Massachusetts. Undergraduate thesis, Harvard University, Cambridge, MA.

Goldstein, P. Z. 1997. Review of: Tuskes, Tuttle, and Collins. The wild silk moths of North America. J. New York Ent. Soc. 105(1-2): 121-125.

Harris, T. W. (C. L. Flint, ed.) 1890. Treatise on some of the insects injurious to vegetation. New York: Orange Judd Co. 640 pp. [2nd edition of: Harris, T. W. 1841. A report on the insects of Massachusetts, injurious to vegetation. Cambridge, MA: Folsom, Wells and Thurston.]

Hayes, J. L. 1983. A comparison of the life history and morphological character patterns in temperate butterflies. J. Kans. Ent. Soc. 56: 547-551.

Hessel, S. A. 1976. A preliminary scan of rare and endangered Nearctic moths. Atala 4: 19-21.

Holloway, J. D. & P. D. N. Herbert. 1979. Ecological and taxonomic trends in macrolepidopteran host plant selection. Biol. J. Linn. Soc. 11: 229-251.

House, H. L. 1962. Insect nutrition. Ann. Rev. Biochem. 31: 653-672.

Howard, L. O. & W. F. Fiske. 1911. The importation into the United States of the parasites of the gipsy-moth and the browntail moth. USDA Bur. Entomol. Bull. 1911, 1.

James, T. D. W. & D. W. Smith. 1978. Seasonal changes in the major ash constituents of leaves and some woody components of trembling aspent and red osier dogwood. Can. J. Bot. 56: 1798-1803.

Jermy, T. 1984. Evolution of insect/host plant relationships. Am. Nat. 124: 609-630.

Jones, F. M. & C. P. Kimball. 1943. The Lepidoptera of Nantucket and Martha's Vineyard Islands, Massachusetts. The Nantucket Maria Mitchell Association. Vol. IV. Nantucket, MA.

Lemaire, C. 1988. The Saturniidae of America. Ceratocampinae. Museo Nacional de Costa Rica, San Jose.

Little, S. 1979. Fire and plant succession in the New Jersey Pine Barrens. Pp. 297-314. *In*: Forman, R. T. T. (ed.). Pine Barrens: ecosistem and landscape. Orlando, FL: Academic Press.

Mattson, W. J. 1977. Size and abundance of forest Lepidoptera in relation to host plant resources. Colloques Internationaux du C.N.R.S. 265: 429-441.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119-161.

Mattson, W. J. & J. M. Scriber. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. Pp. 114-139. *In*: F. Slansky and J. G. Rodriguez (eds.), Nutritional ecology of insects, mites, spiders, and related invertebrates. John Wiley and Sons, New York.

Mello, M., M. Aliberti, S. Galusha, K. Gerber, F. Hohn, A. Lawrence, D. Luers, R. J. Nagel, T. Ruehli & B. Stephenson. 1999. Lloyd Center for Environmental Studies. Inventory of state-listed Lepidoptera and other insects at Massachusetts Military Reservation 1996-1998. Report to Massachusetts Natural Heritage & Endangered Species Program.

Michener, C. D. 1950. A northern subspecies of *Eacles imperialis* (Lepidoptera: Saturniidae). Jour. Kans. Ent. Soc. 23: 17-21.

Miller, P. C. & W. A. Stoner. 1979. Canopy structure and environmental interactions. Pp. 428-458. *In*: O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven (eds.), Topics in plant population biology. New York: Columbia University Press.

Mousseau, T. A. & H. Dingle. 1991. Maternal effects on insect life histories. Ann. Rev. Entomol. 36: 511-534.

Niemela, P., S. Hanhimaki, & R. Mannila. 1981. The relationship of adult size in noctuid moths (Lepidoptera: Noctuidae) to breadth of diet and growth form of host plants. Annales Entomologici Fennici 47: 17-20.

Opler, P. A. 1978. Interaction of plant life history components as related to arboreal herbivory. Pp. 23-32. *In*: G. G. Montgomery (ed.), Ecology of Arboreal Folivores. Washington, D.C.: Smithsonian Institute.

Patch, E. M. 1908. Insect notes for 1908. Maine Agric. Exp. Stn. Bull. 162: 351-387.

Peters, R. H. 1983. The ecological implications of body size.

Cambridge: Cambridge University Press.

RAFFA, K. F. 1991. Induced defensive reactions in conifer-bark beetle systems. Pp. 245-276. *In:* D. W. Tallamy and M. J. Raupp (eds.) Phytochemical induction by herbivores. New York: Academic Press.

SCHWEITZER, D. F. 1983. Rare Lepidoptera of the Katama Plain on Martha's Vineyard, Massachusetts. Report to Massachusetts Natural Heritage and Engangered Species Program, Boston.

SCHWEITZER, D. F. 1988. Status of Saturniidae in the northeastern USA: a quick review. News of the Lepidopterists' Society [1988] 1: 2-3.

SCHWEITZER, D. F. & T. J. RAWINSKI. 1988. TNC Element stewardship abstract: northeastern itch pine/scrub oak barrens. The Nature Conservancy, Eastern Heritage Task Force, Boston, MA.

SCHROEDER, L. A. 1984. Comparison of gravimetry and planimetry in determining dry matter budgets for three species of phytophagous lepidopteran larvae. Entomol. Appl. 35: 255-261.

SCRIBER, J. M. 1977. Limiting effect of low-leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Oecologia 28: 269-287.

SCRIBER, J. M. 1978. The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: an ecological consideration. Ent. Exp. App. 24: 694-710.

SCRIBER, J. M. 1979a. The effects of sequentially switching foodplants upon biomass and nitrogen utilization by polyphagous and stenophagous *Papilio* larvae. Ent. Exp. Appl. 25: 203-215.

SCRIBER, J. M. 1979b. Effects of leafwater supplementation upon postingestive nutritional indices of forb, shrub, vine, and treefeeding Lepidoptera. Ent. Exp. Appl. 25: 240-252.

SCRIBER, J. M. 1983. The evolution of feeding specialization, physiological efficiency, and host races in selected Papilionidae and Saturniidae. Pp. 373-412. *In:* Denno, R. F. and M. S. McClure (eds.), Variable plants and herbivores in natural and managed systems. New York: Academic Press.

SCRIBER, J. M. & P. FEENY. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. Ecology 60: 829-850.

SCRIBER, J. M. & F. SLANSKY. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol. 26: 183-211.

SLANSKY, F. & J. M. SCRIBER. 1985. Food consumption and utilization. Pp. 87-163. *In:* G. A. Kerkut and L. I. Gilbert (eds.), Comprehensive Insect Physiology, Biochemistry, and Pharmacology Vol. 4. Pergamon Press.

STONE, S. E. 1991. Foodplants of world Saturniidae. Lepid. Soc. Memoir 4. Lepidopterists' Society, Lawrence, Kans.

TILTON, D. L. 1977. Seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems. Can. J. Bot. 55: 1291-1298.

TUSKES, P. M., J. P. TUTTLE, & M. M. COLLINS. 1996. The wild silk moths of North America. A natural history of the saturniidae of the United States and Canada. Ithaca: Cornell University Press.

WALDBAUER, G. P. 1968. The consumption and utilization of food by insects. Advances in Insect Physiology 5: 229-288.

WASSERMAN, S. S. & C. MITTER. 1978. The relationship of body size to breadth of diet in some Lepidoptera. Ecol. Ent. 3: 155-160.

WEBBER, R. T., & J. V. SCHAFFNER JR. 1926. Host relations of *Compsilura concinnata* Meigen, an important tachinid parasite of the gipsy moth and the brown-tail moth. Washingon D. C., USDA bulletin 1363.

WIKLUND, C. 1975. The evolutionary relationships between adult oviposition preference and larval host plant range in *Papilio machaon* L. Oecologia 18: 185-197.